

# The group selection debate and ALife: weak altruism, strong altruism, and inclusive fitness

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Models of the evolution of social behaviour are often framed in terms of either multi-level selection or inclusive individual fitness theory. Although both of these descriptions correctly predict changes in gene frequency (where group fitness is defined as the average individual fitness of the group members), it is still a hotly contested issue as to which provides a faithful description of the underlying causal processes at work. Furthermore, the type of model analysis used reflects the philosophical bias of the author. It is important for ALife researchers to be aware of this issue when evaluating or presenting models of social evolution, for many authors simply claim as a matter of fact that their model works via multi-level or (inclusive) individual selection, without acknowledging the alternative perspective.

In this talk, two particular areas of ongoing contention between multi-level and individual selectionists will be illustrated, using examples from the ALife literature. The first of these concerns the evolution of weakly altruistic traits. These are behaviours that provide a whole-group benefit at some cost to the actor. Crucially, however, the cost to the actor is more than offset by its share of the group benefit, such that the lifetime number of offspring of the actor is increased. In a recent paper West et al. (2007, *J. Evol. Biol.*, 20, p.415) have advocated that the evolution of such traits can be adequately explained in terms of direct fitness benefit, thus avoiding the need to invoke selection at the group level. However, this explanation hides the fact that weak altruists suffer a relative fitness disadvantage within every group. Indeed, the local attractor within any one group is the extinction of weak altruists. Therefore, the behaviour cannot spread unless groups compete and groups with more weak altruists are fitter than those with less. While the individualist methodology correctly predicts if the behaviour will evolve, it obscures the mechanistic explanation. This suggests that models couching the evolution of social behaviour in terms of individual benefit should be analysed to determine whether group structure is playing any causal role in the evolutionary dynamics.

The second issue to be addressed by this talk concerns the evolution of strong altruism, i.e., behaviours where there is a reduction in the lifetime number of offspring of the actor. For such behaviours to evolve there must be a correlation in interactions, such that the recipients of an altruist's help tend to be altruists themselves. This correlation frequently occurs in nature through the limited dispersal of kin, and is usually modelled by inclusive fitness equations that contain no notion of group fitness. However, the underlying mechanism is that kin groups with more altruists outcompete those with less. Once this is realised, it becomes apparent that other assortative group formation mechanisms can in principle produce the same effect. Appealing to kinship is therefore simply invoking one kind of assortative grouping.

This talk will further elaborate on these points, including definitions of a group, and consider claims about the strength of group selection.